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Recognition of *Mycena* sect. *Amparoina* sect. nov. (Mycenaceae, Agaricales), including four new species and revision of the limits of sect. *Sacchariferae*

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Abstract

Phylogenetic reconstruction revealed that *Mycena* stirps *Amparoina*, which is traditionally classified in sect. *Sacchariferae*, should be treated at section level. Section *Amparoina* is characterised by the presence or absence of cherocytes, the presence of acanthocysts and spinulose caulocystidia. Eight species referred to *Mycena* sect. *Amparoina* **sect. nov.** are recognised in China. Of these taxa, four new species classified in the new section are formally described: *M. bicystidiata* **sp. nov.**, *M. griseotincta* **sp. nov.**, *M. hygrophoroides* **sp. nov.** and *M. miscanthi* **sp. nov.** The new species are characterised by the absence of both cherocytes and a basal disc, along with the presence of acanthocysts on the pileus, spinulose cheilocystidia and caulocystidia. Descriptions of the new species, accompanied by illustrations of morphological characters and comparisons with closely related taxa, are provided. A multi-locus analysis utilising the ITS + nLSU + SSU regions was carried out using maximum likelihood and Bayesian Inference. A key to the 12 species of sect. *Amparoina* **sect. nov.** and sect. *Sacchariferae* that are found in China is provided.

Keywords

Agarics, new taxon, systematics, taxonomy

Introduction

The genus *Mycena* (Pers.) Roussel is characterised by small basidiomata, thin and convex pileus with sulcate margin, non-deliquescent lamellae and hollow stipe (Persoon 1797). The genus comprises more than 500 species and is distributed worldwide (Kirk

et al. 2008). *Mycena* sect. *Sacchariferae* Kühner ex Singer, which is one of the largest sections in the genus, was first published as a *nomen nudum* by Kühner (1938), who defined the section to include members that possess a granulose or "sugar coated" pileus. In 1958, Singer erected the monotypic genus *Amparoina* Singer to house *Marasmius spinosissimus* Singer based on the collections from Argentina (Singer 1958). Later, Singer (1976) established Amparoinaceae with *A. spinosissima* (Singer) Singer as type species and introduced another species in *Amparoina*, *A. heteracantha* Singer. Meanwhile he suggested that *Amparoina* was similar to sect. *Sacchariferae*, but maintained the autonomy of the former due to inamyloid basidiospores and revised sect. *Sacchariferae* to be characterised by a pileipellis with acanthocysts, which remain as terminal cells overlaid by a universal veil (Singer 1976). The pileus of cherocytes and acanthocysts distinguish taxa of sect. *Sacchariferae* from all other *Mycena* species. Section *Sacchariferae* was subdivided by Desjardin (1995) into stirps *Amparoina* Desjardin, stirps *Alphitophora* Desjardin and stirps *Adscendens* Desjardin, with 55 epithets classified into 27 taxa, based on presence or absence of a basal disc, cherocytes, and diverse caulocystidia. Maas Geesteranus and de Meijer (1997) established a fourth stirps, named stirps *Fuscinea* Maas Geest. & de Meijer, in which the acanthocysts possess brown contents, a character similar to that of stirps *Amparoina*. Only two species have been classified in stirps *Fuscinea*, namely *M. fuscinea* Maas Geest. & de Meijer and *M. fuliginea* Maas Geest. & de Meijer (Maas Geesteranus and de Meijer 1998). The morphology-based infrasectional classification of *Mycena* sect. *Sacchariferae*, proposed by Desjardin (1995), has been widely adopted. However, no phylogenetic reconstruction of relationships in sect. *Sacchariferae* has been published to assess the validity of the infrasectional classification.

Previous studies of sect. *Sacchariferae* have focused on species distributed in Europe and North and South America, with more than 60 species studied in the past 30 years (Maas Geesteranus 1983, 1992a, 1992b; Lodge 1988; Takahashi 1999; Perry 2002; Grgurinovic 2003; Robich 2003, 2016; Tanaka and Hongo 2003; Nealel 2009; Robich and Hausknecht 2009; Zamora and Català 2013; Cortéspérez et al. 2015; Aronsen and Læssøe 2016). In contrast, studies of Asian taxa have been scanty until recent years. Aravindakshan and Manimohan (2015) described ten taxa, including six new species in sect. *Sacchariferae* from India. Only three species, *M. anoectochili* L. Fan & S.X. Guo, *M. alphitophora* (Berk.) Sacc. and *M. cornephora* Maas Geest., were formerly reported from China (Guo et al. 1997; Li et al. 2015). However, recently, three new taxa of sect. *Sacchariferae* were described, namely *M. castaneicola* T. Bau & Q. Na, *M. hyalinostipitata* T. Bau & Q. Na and *M. substylobates* T. Bau & Q. Na, from subtropical regions of China (Na and Bau 2019).

A phylogenetic reconstruction of *Mycena* was incongruous with the traditional classification of stirps *Amparoina* within sect. *Sacchariferae* and indicated that the taxonomic classification of the section should be reconsidered. During our ongoing research on *Mycena*, four new taxa without a basal disc and cherocytes, belonging to the new section, were found in southern China in Chongqing City, Guangdong Province,

Henan Province, Hubei Province, Tibet Autonomous Region, Yunnan Province and Zhejiang Province. These species are described here. Based on the phylogenetic analyses, an identification key to the 12 species of sect. *Sacchariferae* and sect. *Amparoina* currently known from China is provided.

Materials and methods

Morphological study

Macroscopic characters were described from fresh specimens following conventional taxonomic methods. Colour terms and notations refer to those of Kornerup and Wanscher (1978). Microscopic characters were observed from dried specimens rehydrated in 5% potassium hydroxide (KOH) and stained with Congo red, using a Nikon 80i light microscope. Melzer's reagent was used for testing amyloid and dextrinoid reactions of all tissues (Horak 2005). The spore shape quotient (spore length divided by spore width; $Q = L/B$) was calculated from 40 mature basidiospores; 90% of the numerical range is indicated outside parentheses and the 10% extreme values are enclosed in parentheses. Author abbreviations are based on those used in Index Fungorum (https://www.indexfungorum.org). Voucher specimens have been deposited in the Herbarium Mycology of Jilin Agricultural University (HMJAU).

DNA extraction, PCR amplification and DNA sequencing

Material for DNA isolation was taken from dried specimens. Genomic DNA was extracted from samples using the NuClean Plant Genomic DNA Kit (Kangwei Century Biotechnology Company Limited, Beijing, China). The internal transcribed spacer (ITS) region was amplified with the primer pair ITS1 and ITS4 (White et al. 1990). The nLSU and SSU regions were amplified using the primers LROR/LR7 and MS1/MS2, respectively (Ward et al. 1992; Hopple and Vilgalys 1999). The PCR cycling schedule for the ITS, nLSU and SSU region used a touchdown programme (Na and Bau 2018). All newly generated sequences were deposited in GenBank (Table 1).

Sequence alignment and phylogenetic analysis

A dataset, comprising sequences for the ITS + nLSU + SSU region from 96 accessions with taxonomic coverage of Europe, North America, Australia, Africa and Asia, was compiled and analysed. Sequences for 32 accessions were downloaded from GenBank and 64 newly generated sequences obtained in this study were aligned and adjusted manually using BioEdit 7.0.4.1 and Clustal X (Thompson et al. 1997;

Table 1. Sequenced specimens used in phylogenetic analysis.

Taxa	Voucher	Locality	GenBank accession no.		
			ITS	nLSU	SSU
Infundibulicybe gibba (Pers.) Harmaja	AFTOL-ID 1508	USA	DQ490635	DQ457682	–
I. gibba	FLAS-F-60947	Unpublished	MH016906	–	–
Mycena abramsii (Murrill) Murrill	HMJAU 43282	Jilin: Jingyuetan National Scenic Area, Changchun City	MH396626	MK629348	MK629326
M. abramsii	HMJAU 43468	Jilin: Jingyuetan National Scenic Area, Changchun City	MH396627	–	MK629328
	HMJAU 43523	Jilin: Songjiang Town, Jiaohe City	MH396628	MK629350	MK629330
	HMJAU 43606	Inner Mongolia Autonomous Region: Mangui Town, Hulunbeier City	MH396629	MK629355	MK629336
M. adscendens Maas Geest.	Orstadius329-05	Norway: Strengsdal Village, Vestfold	KT900141	–	–
M. adscendens	Aronsen061119	Norway: Strengsdal Village, Vestfold	KT900142	–	–
	Aronsen120826	Norway: Strengsdal Village, Vestfold	KT900143	–	–
M. alphitophora	HMJAU 43498	Jilin: Shenglihe forest farms, Jiaohe City	MH136830	–	MK629329
	HMJAU 43686	Yunnan: Zixi Mountain National Nature Reserve, Chuxiong City	MH136831	–	MK629343
M. arcangeliana Bres.	252b	Italy: Venice Museum of Natural History, Venice	JF908401	–	–
M. arcangeliana	252f	Italy: Venice Museum of Natural History, Venice	JF908402	–	–
M. bicystidiata T.Bau & Q.Na	HMJAU 43589	Hubei: Yandongwan, Lichuan County	MK309774	–	–
M. bicystidiata	HMJAU 43593	Hubei: Xingdou Mountain National Nature Reserves	MK309775	MK629354	–
	HMJAU 43648, **Type**	Chongqing: Dafengbao Scenic Regions, Huangshui Town	MK309773	MK629359	MK629341
	HMJAU 43744	Zhejiang: Tianmu Mountain National Nature Reserves, Hangzhou City	MK309776	–	–
M. castaneicola T.Bau & Q.Na	HMJAU 43578, **Type**	Henan: Jigong Mountain National Nature, Xinyang City	MH136826	–	MK629334
M. castaneicola	HMJAU 43581	Henan: Bolden National Forest Park, Xinyang City	MH136827	–	–
M. citrinomarginata Gillet	HMJAU 43563	Shanxi: Wutai Mountain National Nature, Xinzhou City	MG654739	MK629351	MK629331
M. citrinomarginata	317h	Italy: Venice Museum of Natural History, Venice	JF908416	–	–
	AD4TN	Tunisia: Aïn Draham	KU973883	–	–
M. corynephora Maas Geest.	HMJAU 43574	Henan: Xinyang City	MH136832	–	MK629332
M. corynephora	HMJAU 43576	Henan: Xinyang City	MH136833	–	MK629333
M. diosma Krieglst.&Schwöbel	320f	Italy: Venice Museum of Natural History, Venice	JF908417	–	–
M. griseotincta T.Bau & Q.Na	HMJAU 43800, **Type**	Yunnan: Shangri-La Pudacuo National Park	MK309783	MK629363	MK629346
M. griseotincta	HMJAU 43805	Yunnan: Shangri-La Pudacuo National Park	MK309782	–	–
	HMJAU 43819	Tibet: Zhuqudeng Village, Nyingchi City	MK309784	–	–
M. heteracantha (Singer) Desjardin	HMJAU 43709,	Hunan: Yuelu Mountain, Changsha City	MK309785	MK629362	MK629345
M. heteracantha	HMJAU 43711	Hunan: Xiaoxi National Nature Reserves	MK309786	–	–
	HMJAU 43716	Hunan: Gaowangjie National Nature Reserves	MK309787	–	–
M. hyalinostipitata T.Bau&Q. Na	HMJAU 43693, **Type**	Yunnan: Yeyahu Scenic Spot, Kunming City	MH136828	MK629361	MK629344

Taxa	Voucher	Locality	GenBank accession no.		
			ITS	nLSU	SSU
M. hyalinostipitata	HMJAU 43701	Yunnan: Yeyahu Scenic Spot, Kunming City	MH136829	–	–
M. hygrophoroides	HMJAU 43417, **Type**	Guangdong: Chebaling National Nature Reserve, Shaoguan City	MK309780	MK629349	MK629327
	HMJAU 43421	Guangdong: Shangxie Village, Shaoguan City	MK309781	–	–
M. meliigena (Berk.&Cooke) Sacc.	39	Italy: Venice Museum of Natural History, Venice	JF908423	–	–
M. meliigena	39d	Italy: Venice Museum of Natural History, Venice	JF908429	–	–
M. miscanthi T.Bau & Q.Na	HMJAU 43573	Henan: Jinniu Mountain, Xinyang City	MK309777	MK629352	–
M. miscanthi	HMJAU 43582	Henan: Bolden National Forest Park, Xinyang City	MK309778	–	–
	HMJAU 43584, **Type**	Henan: Jigong Mountain National Nature, Xinyang City	MK309779	MK629353	MK629335
M. pearsoniana Dennis ex Singer	FCME25817	USA: Great Smoky Mountains National Park, Tennessee	JN182198	–	–
M. pearsoniana	TENN61544	USA: Great Smoky Mountains National Park, Tennessee	JN182199	–	–
	TENN61384	USA: Great Smoky Mountains National Park, Tennessee	JN182200	–	–
M. pelianthina (Fr.) Quél.	108b	Italy: Venice Museum of Natural History, Venice	JF908379	–	–
M. pelianthina	108f	Italy: Venice Museum of Natural History, Venice	JF908380	–	–
	CBH164	Denmark: Jutland, Paderup Mose	FN394548	–	–
M. pseudocorticola Kühner	124a	Italy: Venice Museum of Natural History, Venice	JF908386	–	–
M. pura (Pers.) P. Kumm.	HMJAU 43121	Liaoning: Ant Ridge, Dandong City	MK309793	–	–
M. pura	HMJAU 43179	Heilongjiang: Shengshan National Nature Reserve	MK309794	–	–
	TENN65043	USA: Great Smoky Mountains National Park, Tennessee	JN182202	–	–
M. rosea Gramberg	CBH409	Germany: Baden-Württemberg, Schwarzwald	FN394551	–	–
M. rosea	TL12409	Denmark: Jutland, Skivum Nørrekrat	FN394557	–	–
M. rosella (Fr.) P. Kumm.	938a	Italy: Venice Museum of Natural History, Venice	JF908488	–	–
M. rosella	Champ-21	JGI MycoCosm database	KX449424	–	–
M. seminau A.L.C.Chew&Desjardin	ACL136	Malaysia: Ulu Gombak, Selangor	KF537250	–	–
M. seminau	ACL308	Malaysia: Ulu Gombak, Selangor	KF537252	–	–
M. silvae-nigrae Maas Geest.&Schwöbel	515	Italy: Venice Museum of Natural History, Venice	JF908452	–	–
M. silvae-nigrae	CC 13-12	USA: Great Smoky Mountains National Park	KF359604	–	–
M. substylobates T.Bau & Q.Na	HMJAU 43418, **Type**	Guangdong: Chebaling National Nature Reserve, Shaoguan City	MH216189	–	–
M. substylobates	HMJAU 43444	Guangxi Zhuang Autonomous Region: Nonggang National Nature Reserve, Chongzuo City	MH216190	–	–
M. supina (Fr.) P. Kumm.	128a	Italy: Venice Museum of Natural History, Venice	JF908388	–	–
M. tenerrima Maas Geest.	HMJAU 43646	Chongqing: Huangshui Town	MK309795	–	MK629340
M. tenerrima	HMJAU 43816	Tibet: Bomi County, Nyingchi City	MK309796	MK629364	–
M. zephirus (Fr.) P. Kumm.	CBS 270.48	Netherlands: Microbial Biological Resource Centres	MH856339	–	–
M. zephirus	CBS 273.48	Netherlands: Microbial Biological Resource Centres	MH856341	–	–

Hall 1999). The alignment was deposited with TreeBase (submission ID, 24326; study accession URL: http://purl.org/phylo/treebase/phylows/study/TB2:S24326). *Infundibulicybe gibba* were chosen as the outgroup. The aligned dataset consisted of 817 ITS, 1530 nLSU and 620 SSU nucleotide sites (including gaps). The best-fit evolutionary model was identified using Modeltest 2.3 for each of the ITS, nLSU and SSU data partitions for Bayesian Inference (BI), which was implemented with MrBayes 3.2.6 (Ronquist and Huelsenbeck 2003; Nylander 2004). Markov chain Monte Carlo (MCMC) chains were run for one million generations, sampling every 100th generation until the critical value for the topological convergence diagnostic was less than 0.01 (Ronquist and Huelsenbeck 2003). Maximum Likelihood (ML) analysis was performed in raxmlGUI 1.5b1, with a rapid bootstrapping algorithm involving 1,000 replicates (Stamatakis et al. 2004). Topology support values greater than 75% bootstrap support (ML) 0.95 and Bayesian posterior probabilities (BPP) are shown at each branch node.

Results

Phylogeny

Sect. *Amparoina* (Clade 5) formed a distinct clade separated from sect. *Sacchariferae* (Clade 4), sect. *Calodontes* (Clade 3), sect. *Supinaae* (Clade 2) and sect. *Fragilipedes* (Clade 1), as a sister group to all other clades within the ingroup with high statistical support (ML ≥ 75%, BPP ≥ 1.00) and should be elevated to section level.

Phylogenetic reconstructions obtained using BI and ML showed similar topologies. The best-scoring Maximum Likelihood (ML) tree was selected as a representative phylogeny (Fig. 1). The optimal evolutionary model for the 5.8S and nLSU partition were lset nst = 6, rates = invgamma and prset statefreqpr = dirichlet (1,1,1,1) and SSU was lset nst = 6, rates = gamma and prset statefreqpr = dirichlet (1,1,1,1). The phylogenetic tree contained six clades, five including species of *Mycena*. The latter clade was nested within the clades of *Mycena* species. Each of the five clades of *Mycena* species corresponded with a taxonomic section, circumscribed from morphological characters, with high statistical support (ML ≥ 75%, BPP ≥ 0.95).

Samples of the four new species were placed in separate monophyletic lineages, each with high statistical support (*M. bicystidiatum*, ML = 99%, BPP = 1.00; *M. griseotincta*, ML = 99%, BPP = 1.00; *M. hygrophoroides*, ML = 98%, BPP = 0.99; *M. miscanthi*, ML = 100%, BPP = 1.00; Fig. 1). The phylogenetic tree resolved a strongly supported stirps *Alphitophora* comprising these species along with *M. alphitophora* (Berk.) Sacc., *M. corynephora* Maas Geest. in Clade 5 with ML = 100%, BPP = 1.00. Then stirps *Amparoina*, also located in Clade 5 as sister group with stirps *Alphitophora*, formed a monophyletic lineage with high statistical support in accordance with a basal disc in morphology. The distinction of the new taxa from the closely related species, *M. alphitophora* and *M. corynephora*, was also supported.

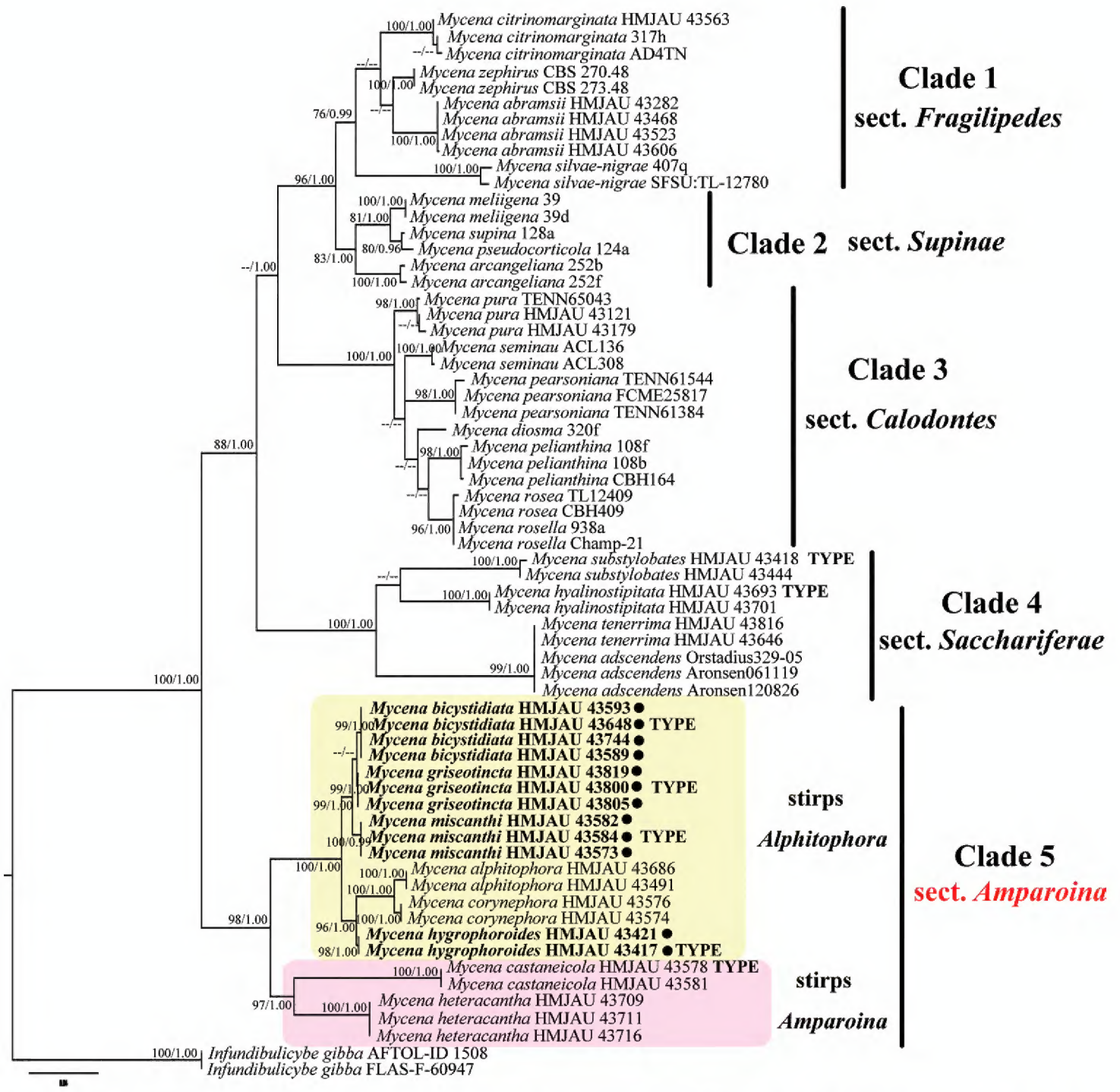

Figure 1. Maximum Likelihood and Bayesian tree concatenated ITS+nLSU+SSU dataset (ML ≥ 75%, BPP ≥ 0.95 are indicated). The tree is rooted with *Infundibulicybe gibba*. The new species are marked by ●.

Taxonomy

Key to species of sect. *Amparoina* and sect. *Sacchariferae* in China

1 Basal disc present, cherocytes absent, acanthocysts present, caulocystidia smooth or with few spines ..... **(sect. *Sacchariferae*) 2**

– Basal disc present or absent, cherocytes present or absent, acanthocysts present, caulocystidia spinulose..... **(sect. *Amparoina*) 5**

2 Pileus grey-black ..... ***M. anoectochila***

– Pileus white **3**

3 Caulocystidia irregularly shaped..... ***M. substylobates***

– Caulocystidia fusiform **4**

4	Cheilocystidia fusiform with spines in the middle part	***M. tenerrima***
–	Cheilocystidia sphaeropedunculate with spines overall	***M. hyalinostipitata***
5	Basal disc and cherocytes present	(**stirps *Amparoina***)**6**
–	Basal disc and cherocytes absent	(**stirps *Alphitophora***)7
6	Habitat on fruits of *Castanea*, pileus slightly pubescent	***M. castaneicola***
–	Habitat on dead wood or humus layer, pileus with bran-like covering	***M. heteracantha***
7	Lamellae distant, L < 10, I < 3	***M. hygrophoroides***
–	Lamellae normal, L > 15, I > 6	**8**
8	Basidiomata typically grey	***M. griseotincta***
–	Basidiomata white	**9**
9	Caulocystidia of two types, sphaeropedunculate or clavate	***M. bicystidiata***
–	Caulocystidia clavate	**10**
10	Basidiospores globose	***M. corynephora***
–	Basidiospores ellipsoid	***11***
11	Acanthocysts of one type, sphaeropedunculate	***M. miscanthi***
–	Acanthocysts of two types, globose or long-clavate	***M. alphitophora***

Section *Amparoina* T.Bau & Q.Na, sect. nov.
MycoBank: MB829096

Diagnosis. Pileus densely pubescent to furfuraceous. Stipe arising from a well-developed basal disc or base swollen without a basal disc. Cheilocystidia with spines. Cherocystes present or absent. Acanthocysts present and overlying universal veil. Caulocystidia densely spinulose overall, never smooth.

Type species. *Mycena spinosissima* (Singer) Desjardin

Etymology. Name refers to the name of stirps *Amparoina*.

***Mycena bicystidiata* T.Bau & Q.Na, sp. nov.**
MycoBank: MB829097
Figs 2c–d, 3

Diagnosis. Pileus furfuraceous to pruinose. Stipe without basal disc. Basidiospores small, 6.1–7.9 × 3.7–4.6 μm. Cheilocystidia clustered, sphaero-pedunculate to utriform with numerous sharp excrescences. Cherocytes absent. Acanthocysts pyriform to vesicular. Caulocystidia of two types, sphaero-pedunculate or clavate covered with conic spines. Clamps present.

Holotype. CHINA. Chongqing City, Dafengbao Scenic Regions, 15 Aug 2017, Qin Na, HMJAU 43648.

Etymology. Name refers to its two types of caulocystidia.

Description. Pileus 2.8–5.2 mm in diam., conical when young, becoming nearly hemispherical with age, pure white all over, sulcate, translucent-striate, pruinose,

Figure 2. Basidiomata of sect. *Amparoina* species. stirps *Alphitophora*: **a–b** *Mycena alphitophora* (Berk.) Sacc. **c–d** *Mycena bicystidiata* T.Bau & Q.Na **e** *Mycena corynephora* Maas Geest. **f–g** *Mycena griseotincta* T.Bau & Q.Na **h** *Mycena hygroporoides* T.Bau & Q.Na **i** *Mycena miscanthi* T.Bau & Q.Na; stirps *Amparoina*: **j** *Mycena castaneicola* T.Bau & Q.Na **k–m** *Mycena heteracantha* (Singer) Desjardin. Basidiomata of sect. *Saccariferae* species **n–o** *Mycena hyalinostipitata* T.Bau & Q.Na **p–q** *Mycena substylobates* T.Bau & Q.Na **r** *Mycena tenerrima* (Berk.) Quél. (=*Mycena adscendens* Maas Geest.) Scale bars: 10 mm (**a–g, i–m, r**), 5 mm (**h, n–q**). Photographs **a–r** by Qin Na.

furfur-like scattered, margin entire first, then nearly plane and finally fissile. Context very thin and fragile, pure white. Lamellae 0.5 mm thick, narrowly adnate, off-white, concolorous with the sides. Stipe slender, 15–28 × 0.5–1.0 mm, cylindrical, hollow, fragile, pure white, densely pruinose on the whole surface, base swollen and not forming a basal disc, hirsute. Odour and taste inconspicuous.

Basidiospores (5.6-)6.1–7.9(-8.3) × (3.5)3.7–4.6(4.9) μm, Q=1.6–2.0, ellipsoid to oblong-ellipsoid, hyaline, with drops, thin walled, amyloid. Basidia 20–26 × 6–9 μm, clavate, hyaline, 4- or 2-spored. Cheilocystidia 19–32 × 12–18 μm, clustered, sphaero-pedunculate to utriform with numerous sharp spines, thin-walled and hyaline, inamyloid. Pleurocystidia absent. Pileipellis hyphae 4–7 μm wide, weakly dextrinoid; cherocytes absent; a cutis overlaid by elements of universal veil, not in chains; acanthocysts of one type, numerous, pyriform to vesicular, 29–62 × 24–51 μm, inamyloid. Hyphae of the stipitipellis 3–14 μm wide, smooth, dextrinoid; caulocystidia abundant, of two types, utriform, sphaero-pedunculate, 21–85 × 14–66 μm or clavate, long-elliptic, 21–85 × 11–26 μm, densely and evenly spinulose overall, hyaline, thin-walled, inamyloid. Clamps present in all tissues.

Habit and habitat. Solitary to scattered on rotten wood in mixed forests, Bamboos, *Cunninghamia*, *Ginkgo* and *Platycladus* forests.

Other specimens examined. CHINA. Hubei Province, Enshi Tujia and Miao Autonomous Prefecture, Lichuan County, Yandongwan, 19 Jul 2017, Qin Na, HMJAU 43589; Xingdou Mountain National Nature Reserves, 20 Jul 2017, Qin Na, HMJAU 43593; Zhejiang Province, Hangzhou City, Tianmu Mountain National Nature Reserves, 4 Jul 2018, Qin Na and Tolgor Bau, HMJAU 43774.

Remarks. *Mycena bicystidiata* is unique in sect. *Amparoina* stirps *Alphitophora* because of the two types of caulocystidia covered with conic spines. *Mycena alphitophora*, which is the most widely distributed species of sect. *Amparoina*, shows the most morphological similarities to *M. bicystidiatum*; however, the former differs in forming cylindric spores (7.5–10 × 4.5–5.5 μm), sphaero-pedunculate cheilocystidia and caulocystidia that are only clavate in shape (Desjardin 1995). *Mycena depilata* Singer is easily mistaken for *M. bicystidiata* by the stipe without a basal disc and the similar shape and size of spores and cheilocystidia, but *M. depilata* is distinguished from *M. bicystidiata* by its small basidiomata (pileus < 0.3 mm), larger spores (8.5–10 × 4.5–5.2 μm), and long-cylindrical and larger caulocystidia (30–120 × 5–20 μm) (Desjardin 1995). In contrast to *M. bicystidiata*, basidiospores of *M. corynephora*, *M. distincta* (Manim. & Leelav.) Aravind. & Manim., *M. globispora* (Manim. & Leelav.) Aravind. & Manim. and *M. yalensis* Singer are globose or broadly ellipsoid (Desjardin 1995; Aravindakshan and Manimohan 2015). The bright or dark colour on the pileus distinguishes *M. brunneospinosa* Desjardin, *M. incarnativelum* Desjardin and *M. roseotincta* Aravind. & Manim. from *M. bicystidiata* (Desjardin 1995; Aravindakshan and Manimohan 2015). In addition, *M. hemitrichialis* Singer produces caulocystidia that are only partially spinulose (Singer 1989).

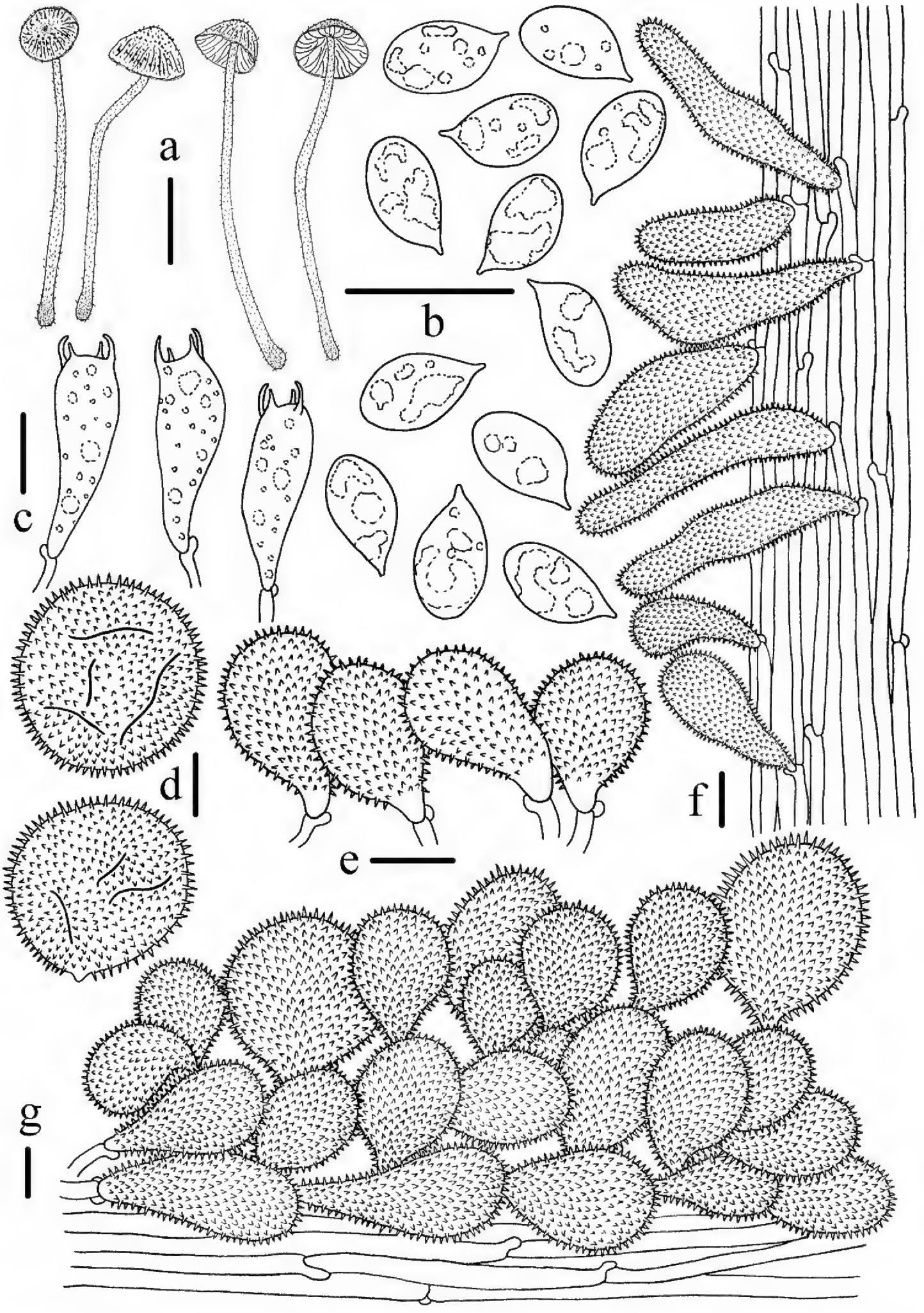

Figure 3. Microscopic features of *Mycena bicystidiata* (HMJAU 43648, holotype) **a** Basidiomata **b** Basidiospores **c** Basidia **d** Universal veil acanthocysts **e** Cheilocystidia **f** Caulocystidia **g** Pileipellis. Scale bars: 5 mm (**a**); 10 μm (**b–g**). Drawing by Qin Na.

Mycena griseotincta **T.Bau & Q.Na, sp. nov.**
MycoBank: MB829098
Figs 2f–g, 4

Diagnosis. Pileus, lamellae and stipe with greyish tint, especially when old. Stipe base swollen. Basidiospores pip-shaped. Pileipellis with two types of acanthocysts. Caulocystidia up to 200 μm long with spines.

Holotype. CHINA. Yunnan Province, Diqing Tibetan Autonomous Prefecture, Shangri-La Pudacuo National Park, 14 August 2018, Qin Na, HMJAU 43800.

Etymology. Name refers to the grey-tinted basidiomata.

Description. Pileus 1.5–12.8 mm in diam., conical when young, campanulate with age, obtusely umbonate in the centre, translucent-striate, white, greyish-white when old (4B1), floccose, pubescent, pruinose, with crenate margin when young, then becoming nearly plane and finely torn. Context pure white, thin, fragile. Lamellae 0.2–0.5 mm thick, narrowly adnate or adnexed, pure white to slightly pale grey (4B1); edges finely torn, concolorous with the sides. Stipe 13–64 × 0.5–1.0 mm, central, terete, almost equal or slightly tapering to apex, hollow, greyish-white (5B1), pubescent or puberulous, with white, fine hairs, base swollen. Odourless, taste mild.

Basidiospores (5.6-)6.3–8.2(-8.5) × (3.5-)4.2–4.6(-5.2) μm, Q=1.5–1.9, Qav=1.7, pip-shaped, hyaline, guttulate, thin walled, amyloid. Basidia 19–23 × 7–9 μm, hyaline, clavate, 4-spored. Cheilocystidia 17–28 × 11–19 μm, oblong or clavate, with short and sharp spines, hyaline, inamyloid. Pleurocystidia absent. Pileipellis hyphae 6–10 μm wide, strongly dextrinoid; cherocytes absent; acanthocysts of two types, pyriform to vesicular, 8–22 × 7–18 μm or clavate to cylindric, 17–51 × 8–13 μm; universal veil composed of acanthocysts, globose, subglobose or sphaero-pedunculate, 28–67 × 26–58 μm, hyaline, covered with long, cylindrical excrescences or long and flexuous spinules, not in chains. Hyphae of the stipitipellis 2–7 μm wide, dextrinoid; caulocystidia abundant, clavate or long cylindrical, 77–216 × 9–11 μm, covered with densely conic spines, inamyloid. Clamps not seen.

Habit and habitat. Scattered to gregarious on litter layer in *Quercus*, *Picea*, *Abies*, *Pinus* mixed forests.

Other specimens examined. Yunnan Province, Diqing Tibetan Autonomous Prefecture, Shangri-La Pudacuo National Park, 15 August 2018, Qin Na, HMJAU 43805; Tibet Autonomous Region, Nyingchi City, Zhuqudeng Village, 20 August 2018, Qin Na, HMJAU 43819.

Remarks. *Mycena griseotincta* is considered a new species in sect. *Amparoina* stirps *Alphitophora* on account of the absence of both a basal disc and cherocytes on the pileal surface (Desjardin 1995). Five species have ellipsoid basidiospores, caulocystidia covered with excrescences and a universal veil composed of acanthocysts: *M. alphitophora*, *M. brunneospinosa*, *M. depilata*, *M. hemitrichialis* and *M. incarnativelum*. *Mycena alphitophora* most resembles *M. griseotincta*, but the former differs in having pure white lamellae, a white and shorter stipe (< 50 mm), sphaero-pedunculate or obovoid cheilocystidia and larger spores (8.1–9.7 × 4.5–5.5 μm), as reported in the original de-

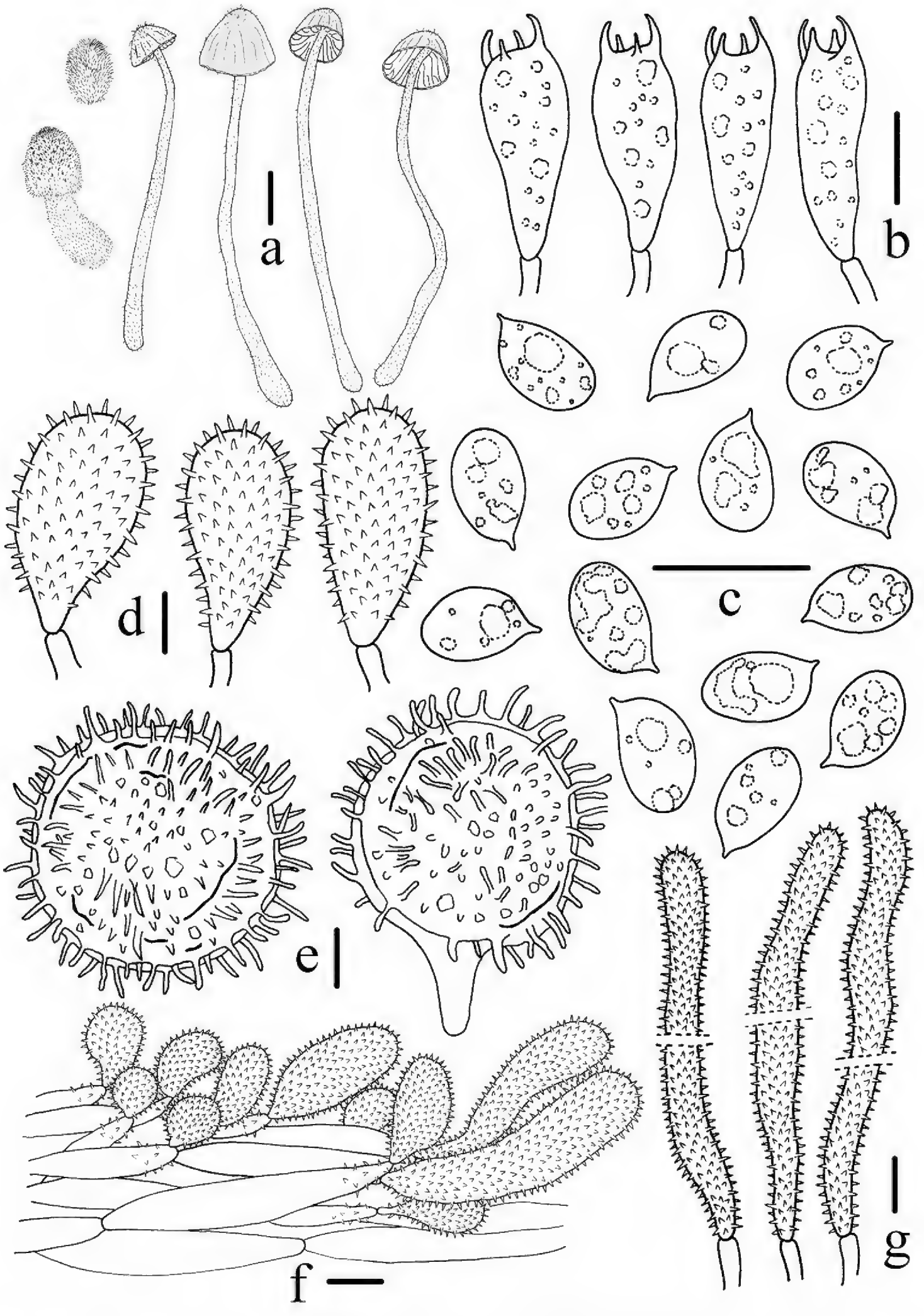

Figure 4. Microscopic features of *Mycena griseotincta* (HMJAU 43800, holotype). **a** Basidiomata **b** Basidia **c** Basidiospores **d** Cheilocystidia **e** Universal veil acanthocysts **f** Pileipellis **g** Caulocystidia. Scale bars: 10 mm (**a**); 10 μm (**b–g**). Drawing by Qin Na.

scription (Maas Geesteranus 1980, 1992b). *Mycena brunneospinosa*, a taxon named by Desjardin (1995), is readily identified by its dull brown or purplish-brown pileus, globose acanthocysts forming chains and broadly ellipsoid spores. *Mycena incarnativelum* is a unique species in sect. *Sacchariferae*, distinguished by the absence of cheilocystidia and deep pink basidiomata when young (Desjardin 1995). *Mycena depilata* is closely allied to *M. griseotincta*, but differs in the convex pileus less than 1 mm in diameter and short and broadly clavate caulocystidia (Singer 1989). *Mycena hemitrichialis* can be mistaken for *M. griseotincta* on account of its grey or pallid pileus and ellipsoid spores, but is distinguished from *M. griseotincta* by its white stipe, free lamellae and pilose stipe forming a flattened ring of mycelium (Desjardin 1995). *Mycena corynephora* is widely distributed worldwide and is recognised by its tiny basidiomata (pileus < 2.4 mm), absence of a basal bulb or basal disc and large globose to subglobose basidiospores, typical of stirps *Alphitophora* (Desjardin 1995; Robich 2003; Aronsen and Læssøe 2016). The same spore shape occurs in *M. yalensis* of which the holotype was collected from Argentina (Singer 1973). Aravindakshan and Manimohan (2015) reported one new species and two others newly combined in *Mycena*, collected from India. The new taxon, *M. roseotincta*, differs from *M. griseotincta* in its pink pileus and universal veil, subcylindrical spores and smaller caulocystidia (Aravindakshan and Manimohan 2015). *Mycena globispora* and *M. distincta* are mainly distinguished in macromorphology from *M. griseotincta* by their white basidiomata and, in micromorphology, by the globose spores and subcylindrical spores, respectively (Aravindakshan and Manimohan 2015).

Mycena hygrophoroides **T.Bau & Q.Na, sp. nov.**
MycoBank: MB829099
Figs 2h, 5

Diagnosis. Pileus concave with slight pruinose. Lamellae distant. Stipe with dense white fibrils and swollen base. Acanthocysts forming two types. Caulocystidia long-elliptic with conical excrescences, up to 120 μm long.

Holotype. CHINA. Guangdong Province, Shaoguan City, Chebaling National Nature Reserve, 8 May 2017, Qin Na, HMJAU 43417.

Etymology. Name refers to its sparse lamellae.

Description. Pileus 1.5–2.5 mm in diam., campanulate to hemispherical, applanate or slightly concave at centre, white with greyish shade (6B1), shallowly sulcate, translucent-striate, slightly pruinose, pubescent. Context white, thin and very fragile. Lamellae distant, sparse, white, concolorous with the sides. Stipe 4.5–8.2 × 0.5–0.8 mm, cylindrical, hollow, fragile, pure white (5A1) with a greyish (5B1) base, covered with dense white fibrils, base swollen and not forming basal disc, hirsute. Odour and taste indistinctive.

Basidiospores (6.9-)7.2-8.9(-9.3) × (5.3-)6.4-6.7(-7.1) μm, Q=1.2–1.5, Qav=1.31, broadly-ellipsoid, hyaline in water and 5% KOH, amyloid, smooth. Basidia 15–21 × 7–9 μm, 4- or 2-spored, clavate, hyaline. Cheilocystidia 23–37 × 19–28 μm, subglo-

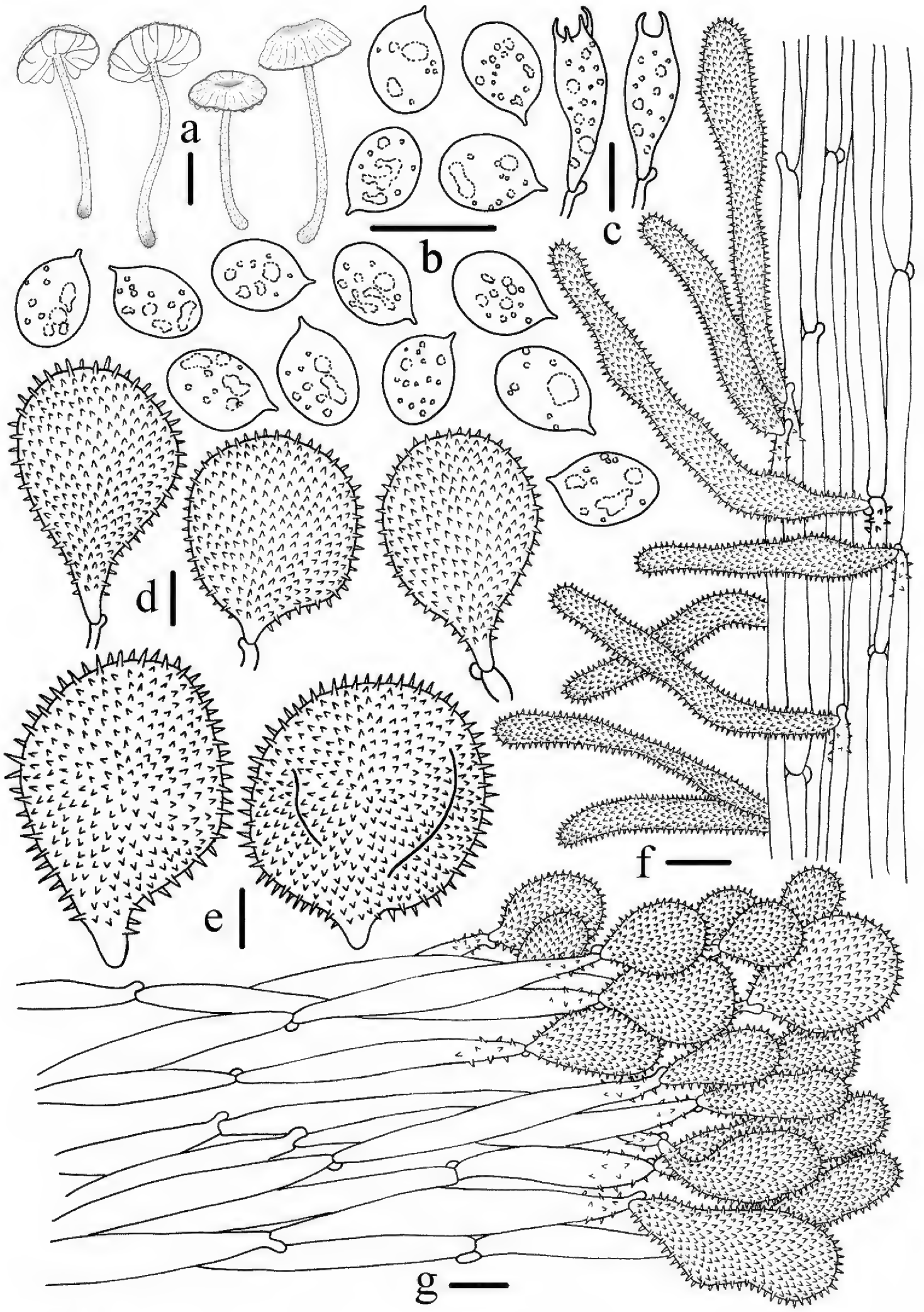

Figure 5. Microscopic features of *Mycena hygrophoroides* (HMJAU 43417, holotype) **a** Basidiomata **b** Basidia **c** Basidiospores **d** Cheilocystidia **e** Universal veil acanthocysts **f** Caulocystidia **g** Pileipellis. Scale bars: 2 mm (**a**); 10 μm (**b–g**). Drawing by Qin Na.

bose, sphaero-pedunculate to utriform with numerous sharp spines, thin-walled and hyaline, inamyloid. Pleurocystidia absent. Pileipellis hyphae 3–9 μm wide, dextrinoid; cherocytes absent; a cutis overlaid by elements of universal veil, not in chains; acanthocysts forming two types, pyriform to vesicular, 13–29 × 11–24 μm, clavate to ovoid or obovoid, 29–42 × 14–20 μm, inamyloid. Hyphae of the stipitipellis 3–7 μm wide, smooth, dextrinoid; caulocystidia abundant, clavate, long-elliptic, 32–122 × 8–11 μm, with numbers of conical spines, inamyloid. Clamps present in all tissues.

Habit and habitat. Scattered on rotten wood of coniferous trees, ex. *Cunninghamia*.

Other specimens examined. Guangdong Province, Shaoguan City, Liangjiang Town, Shangxie Village, 7 May 2017, Qin Na, HMJAU 43421.

Remarks. *Mycena hygrophoroides* could be considered to be a member of *Hemimycena* Singer owing to the tiny basidiomata and sparse lamellae, but the absence of a basal disc, amyloid spores and spinulose cheilocystidia, acanthocysts and caulocystidia are diagnostic characters for *M. hygrophoroides*, which should be placed in *Mycena* sect. *Amparoina* stirps *Alphitophora*. *Mycena acanthophila* J.C.Zamora&Català, of which the holotype was collected from Spain growing on dead branches of Leguminosae, most resembles *M. hygrophoroides*, but differs in having a yellow pileus, smaller cheilocystidia (13.5–22 × 8.5–12 μm) and diverse caulocystidia (Zamora and Català 2012). *Mycena depilata*, a species of stirps *Alphitophora*, shows some morphological similarities to *M. hygrophoroides* in possessing white and tiny basidiomata, distant lamellae (L = 7–9) and globose-pedicellate acanthocysts with hyaline contents. However, *M. depilata* differs in producing ellipsoid spores (Q = 1.64 ± 0.11), broadly clavate cheilocystidia and shorter caulocystidia (16–50 × 5–16 μm; Singer 1989). *Mycena hemitrichialis* is difficult to distinguish from *M. hygrophoroides*, but *M. hemitrichialis* has free to subfree lamellae, longer caulocystidia (100–300 × 5–15 μm) and ellipsoid spores (Singer 1989). In comparison with *M. hygrophoroides*, *M. alphitophora* and *M. distincta* have larger basidiomata and longer caulocystidia of more than 400 μm and 300 μm, respectively (Desjardin 1995; Aravindakshan and Manimohan 2015). Their noticeably pigmented pileus enables discrimination of *M. brunneospinosa*, *M. incarnativelum* and *M. roseotincta* from *M. hygrophoroides* (Desjardin 1995; Aravindakshan and Manimohan 2015). The significantly larger basidiomata and globose spores can be used to distinguish *M. corynephora*, *M. globispora* and *M. yalensis* from *M. hygrophoroides*.

***Mycena miscanthi* T.Bau & Q.Na, sp. nov.**

MycoBank: MB829100

Figs 2i, 6

Diagnosis. Growing on dead stem of *Miscanthus*. Pileus sparsely pruinose. Basidiospores cylindric. Cherocytes absent. Acanthocysts forming two types. Caulocystidia sphaero-pedunculate covered with spines. Clamps present.

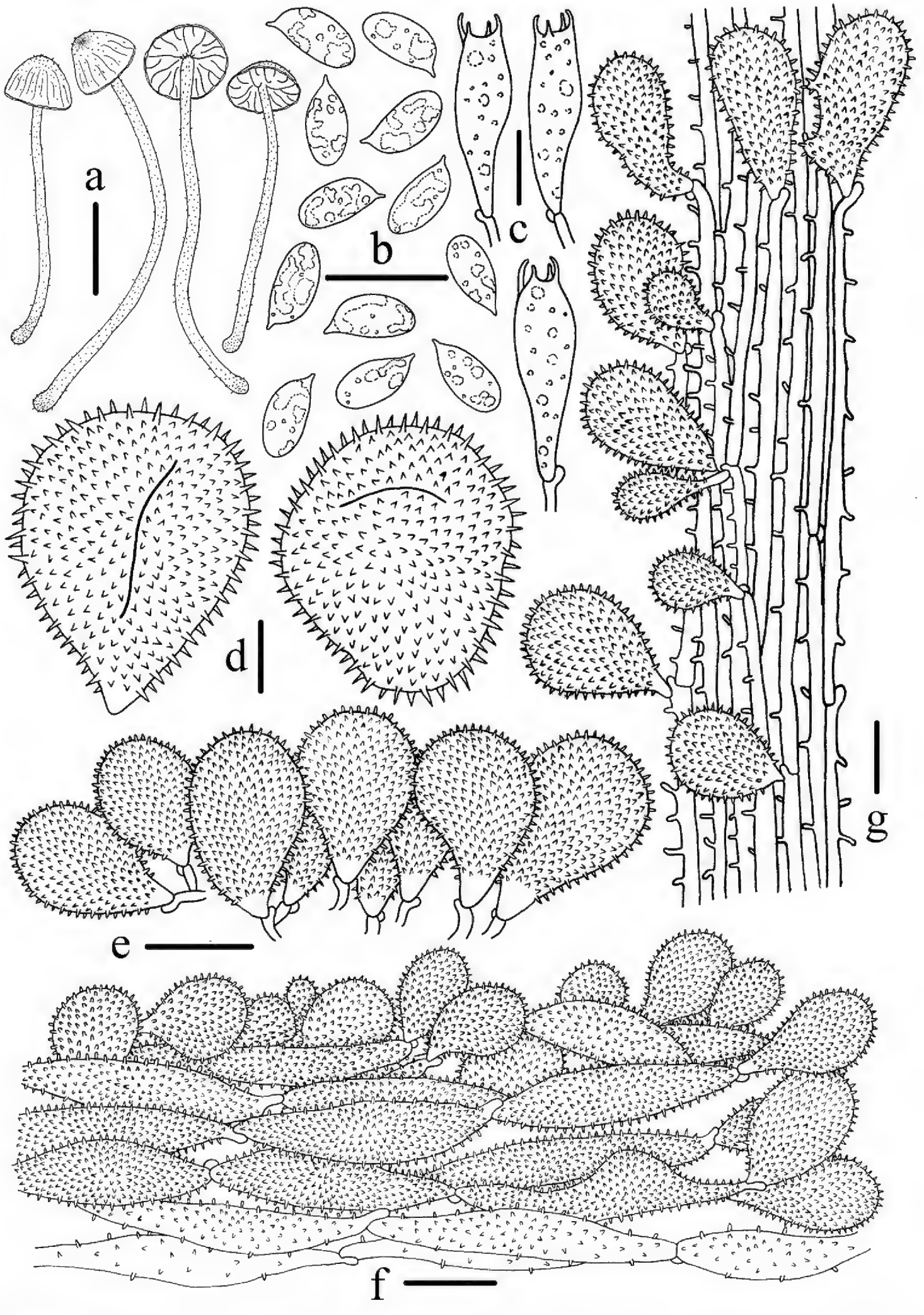

Figure 6. Microscopic features of *Mycena miscanthi* (HMJAU 43584, holotype) **a** Basidiomata **b** Basidiospores **c** Basidia **d** Universal veil acanthocysts **e** Cheilocystidia **f** Pileipellis **g** Caulocystidia. Scale bars: 10 mm (**a**); 10 μm (**b–g**). Drawing by Qin Na.

Holotype. CHINA. Henan Province: Xinyang City, Jigong Mountain, 16 Jul 2017, Qin Na and Tolgor Bau, HMJAU 43584.

Etymology. Name refers to the substratum where the new species was found.

Description. Pileus 3.5–7.8 mm in diam., hemispherical, broadly conical to convex, occasionally ± centrally depressed when young, sulcate, translucent-striate, pure white, pubescent to inconspicuously puberulous, margin nearly plane, undulate. Context white, thin, very fragile, about 1.0 mm thick at centre. Lamellae narrowly adnate or adnexed, off-white, concolorous with the sides. Stipe 26–38 × 0.5–1.0 mm, pure white, central, terete, hollow, equal, surface covered with slight white pubescent, base swollen but not discoid, pruinose. Odour and taste not distinctive.

Basidiospores (6.2-)6.7–8.6(-9.1) × (3.1)3.3–4.2(4.5) μm, Q=1.8–2.3, Qav=2.07, cylindric to narrow-ellipsoid, hyaline, guttulate, thin walled, amyloid. Basidia 18–24 × 6–9 μm, clavate, hyaline, 4-spored. Cheilocystidia 13–26 × 9–14 μm, abundant, lageniform, utriform or sphaero-pedunculate, with short and conical spines. Pleurocystidia absent. Pileipellis hyphae 3–8 μm wide, strongly dextrinoid; cherocytes absent; universal veil composed of acanthocysts, forming two types, pyriform, vesicular or clavate, 12–32 × 10–17 μm, inamyloid. Hyphae of the stipitipellis 2–8 μm wide, with coarse excrescences, 0.9–2.8 × 0.5–0.9 μm, strongly dextrinoid; caulocystidia abundant, elliptic, utriform, sphaero-pedunculate, 15–37 × 7–15 μm, with conical or cylindrical spines inamyloid. Clamps present in all tissues.

Habit and habitat. Solitary to scattered on dead stem of *Miscanthus*.

Other specimens examined. Henan Province, Xinyang City, Jinniu Mountain, 14 Jul 2017, HMJAU 43573; Xinyang City, Bolden National Forest Park, 17 July 2017, Qin Na and Tolgor Bau, HMJAU 43582.

Remarks. The distinctive features of *Mycena miscanthi* include a white, granulose pileus, a pubescent stipe without forming a basal disc, narrow-ellipsoid spores, two types of acanthocysts and growth on dead stems of *Miscanthus* species. In combination, these features support the placement of *M. miscanthi* in sect. *Amparoina* stirps *Alphitophora*. Similar to *M. miscanthi*, *M. alphitophora* and *M. depilata* produce pure white basidiomata, cylindric spores and sphaero-pedunculate and spinulose cheilocystidia (Desjardin 1995; Aravindakshan and Manimohan 2015). However, the two types of acanthocysts and longer caulocystidia can be used to distinguish *M. alphitophora* and *M. depilata* from *M. miscanthi* (Desjardin 1995). *Mycena hemitrichialis* is closely allied to *M. miscanthi*, but differs in producing caulocystidia up to 400 μm in length that lack spinulae or with a few spinulae in the upper half (Singer 1989). *Mycena distincta*, which was originally described as *M. alphitophora* var. *distincta*, was elevated to species level by Manimohan and Leelavathy (1989). It differs from *M. miscanthi* in producing broadly ellipsoid spores and caulocystidia up to 300 μm in length (Aravindakshan and Manimohan 2015). The pigmented pileus present in *M. brunneospinosa*, *M. incarnativelum* and *M. roseotincta* readily distinguishes these species from *M. miscanthi* (Desjardin 1995; Aravindakshan and Manimohan 2015). *Mycena corynephora*, *M. globispora* and *M. yalensis* of stirps *Alphitophora* are characterised by globose to subglobose spores (Maas Geesteranus 1980; Robich 2003; Aravindakshan and Manimohan 2015; Aronsen and Læssøe 2016).

Discussion

The present phylogenetic analysis showed that sect. *Amparoina* formed a distinct clade independent from sect. *Sacchariferae* with high BPP and BS support. This finding suggests that the presence of caulocystidia with dense spines is the most important character to separate sect. *Amparoina* from sect. *Sacchariferae*. However, in the presence of a basal disc, the species of sect. *Sacchariferae* are similar to stirps *Amparoina* and, in the acanthocysts on the pileus sect. *Amparoina* stirps, *Amparoina* resembles sect. *Sacchariferae*. It can be concluded that the difference in caulocystidia can be used to distinguish sect. *Amparoina* and sect. *Sacchariferae* and the basal disc and cherocytes are the basis of an infrasectional classification of sect. *Amparoina*. Thus, the circumscription of sect. *Sacchariferae* should be revised, for which the diagnostic characters are a well-developed basal disc, cherocytes absent, pileipellis a cutis not overlaid by elements of a universal veil composed of acanthocysts and caulocystidia smooth overall.

In morphology, sect. *Amparoina* and sect. *Sacchariferae* are closely allied with sect. *Polyadelphiae* Singer ex Maas Geest. and sect. *Basipedes* (Fr.) Quél (Desjardin et al. 2003). Species of sect. *Polyadelphiae* lack both ornamented pileipellis elements and a stipe with a basal disc and thus differ from species classified in sect. *Amparoina* and sect. *Sacchariferae*. Section *Basipedes* shares the same habitat and a stipe forming a developed basal disc, but the cheilocystidia are covered with rounded and few excrescences. Morphological characters distinguish sect. *Polyadelphiae* and sect. *Basipedes* from sect. *Amparoina* and sect. *Sacchariferae* and only one ITS sequence for *M. stylobates* (Pers.) P. Kumm. (JF908439) is currently deposited in GenBank.

Morphological characters and molecular evidence support the classification of the four new *Mycena* species as members of sect. *Amparoina* stirps *Alphitophora*. The four species share the same furfuraceous or farinose pileus, swollen stipe base without a basal disc, universal veil composed of acanthocysts and absence of both cherocytes and spinose caulocystidia. *Mycena bicystidiatum* is distinguished from *M. griseotincta*, *M. hygrophoroides* and *M. miscanthi* by producing two types of caulocystidia covered with conic spines. *Mycena griseotincta* is readily discriminated from *M. bicystidiatum*, *M. hygrophoroides* and *M. miscanthi* based on the greyish basidiomata and acanthocysts forming a universal veil with long, cylindrical excrescences. Compared with *M. bicystidiatum*, *M. griseotincta*, and *M. miscanthi*, *M. hygrophoroides* is distinct on account of the sparse lamellae and broadly ellipsoid basidiospores. *Mycena miscanthi* differ from *M. bicystidiatum*, *M. griseotincta* and *M. hygrophoroides* in growing on stems of *Miscanthus* and, in addition, the basidiospores are narrow ellipsoid.

It is worth mentioning that the placement of *M. echinocephala* (G.F. Atk.) Desjardin and *M. cylindrospora* A.H. Sm. remains unclear. The species are tentatively placed in stirps *Alphitophora* because of the lack of a basal disc on the stipe, but their caulocystidia are extraordinary in being smooth, terminated by a spinulose apex or smooth with an amorphous apex (Atkinson 1902; Smith 1947; Desjardin 1993). Both species show obvious differences to the four newly described taxa. Furthermore, *M. cryptomeriicola* Imazeki & Toki is distinctive in producing inamyloid spores and a basal disc, which is unusual for specimens of sect. *Sacchariferae* from Japan (Imazeki and Toki

1995). An additional unusual species, *M. minya* Grgur., which lacks caulocystidia, was reported from Australia (Grgurinovic 2003). No species similar in morphology to *M. cryptomeriicola* and *M. minya* are classified in sect. *Sacchariferae*, so the two species are tentatively accepted in sect. *Sacchariferae*.

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